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On the relationships of the Archegoniata.[1]

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Under the name of Archegoniata are usually included the bryophytes and pteridophytes, but we may also include with them the gymnosperms, as all three groups agree in the presence of an unmistakable archegonium, which while differing in some details has such similarity of structure as to point to an almost certain, although remote, common origin for all three groups.

This homology was first shown by Hofmeister[2] in his remarkable series of investigations upon the higher cryptogams and gymnosperms, and has since been the subject of numerous investigations, so that a great mass of material has accumulated.

Numerous attempts have, of course, been made to trace out the inter-relationships of these groups; but recently a good many new facts have been discovered which may throw a somewhat different light upon these, and it is the intention here to call attention to these, and attempt to point out what their bearing is upon the point in question. In trying to do this, the data assumed are mainly derived from the results of a developmental study of the different forms, coupled with such evidence as the palæontological record has to show. Unfortunately the latter is too fragmentary, as regards the lower forms and the more delicate parts of the higher ones, to be of very much service in the study of these points; still very valuable material has been brought to light, and probably much more will be discovered if a systematic search is made.

It is generally admitted that we are to look for the ancestors of the higher plants among the fresh water green Algæ. On account of the structure of the sexual organs, as well as the occurrence of a sort of protonema, the Characeæ have sometimes been regarded as the nearest approach among existing Algæ to the mosses; but if this is so, the ancestral forms must have been of a much less specialized character than even

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[1] Read before Section F, A. A. A. S., Washington Meeting, August, 1891.

[2] The higher Cryptogamia.

the simplest of living forms, and it seems more probable that of living Algæ, the higher Confervaceæ such as *Coleochæte*, come nearer to this hypothetical form.

The first of the groups with which we have to deal, the Bryophyta, or Muscineæ, is readily divisible into two classes, the liverworts (Hepaticæ), and true mosses (Musci). There has been some controversy as to which of these is nearest the primitive stock, and to the higher plants. A comparison of the two groups will show, however, very strong reasons for considering the Hepaticæ as the more primitive group. Although far outnumbered in species by the true mosses, the Hepaticæ show a much greater diversity of form, both of the gametophyte and sporophyte than is the case with the Musci, which form a remarkably close group with relatively insignificant differences (excepting in the case of *Sphagnum*); and the higher ones, with their very peculiar and highly specialized sporogonium, are evidently very remote from any other group of plants. The Hepaticæ, on the other hand, offer a very strong contrast to this. Several divergent stocks are evident, all traceable to a common form and touching in certain respects, Algæ, Musci, and Pteridophyta. The thallus of such simply organized forms as *Anthoceros* or *Pellia*, is but a slight advance on the higher green Algæ, although it must be borne in mind that this simplicity does not extend to the sexual organs and sporophyte. On the other hand, these same forms are connected directly with the Musci through *Sphagnum*, and as the writer has endeavored to show before,[1] to such pteridophytes as *Ophioglossum*.

If we now study a little more closely the relation of the Hepaticæ, *inter se*, we can distinguish three well-marked series of forms diverging from a common stock. Nearly all liverworts pass through a more or less well-marked thallose stage which is persistent in some of the simpler thallose Jungermanniaceæ such as *Aneura* and *Metzgeria*. This is a simple flat often heart-shaped thallus, growing from a single apical cell. It is usually, although not always, traversed by a well-marked mid-rib. The frequent recurrence of this stage in the development of so many forms of Hepaticæ, as well as in the prothallium of the isosporous ferns, is most readily explained by the assumption that this represents the ancestral type from which both groups have sprung. Granting this to

[1] The affinities of the Filicineæ: Bot. Gaz. Jan., 1890.

be the case, the thallose Jungermanniaceæ are to be regarded as the most primitive of living forms, and not the Ricciaceæ, which are usually so considered. It seems more likely that the latter, together with the very closely related Marchantiaceæ, represent a group in which the thallus has become highly differentiated, without a corresponding development of the sporophyte, and which reaches its highest expression in such forms as *Marchantia* and *Asterella.* Of course it is possible to regard the simpler Ricciaceæ as the primitive forms from which the Jungermanniaceæ have sprung; but this would involve a reduction of the thallus in the latter which seems hardly probable, as in some Marchantiaceæ, and probably in the Ricciaceæ also, the young thallus corresponds closely to to that of the simpler Jungermanniaceæ, and the massive thallus of the older plant arises secondarily. The very simple sporogonium of *Riccia*, of course, is an important point in determining its systematic position, and indicates, that if, as here suggested, the Ricciaceæ are derived from forms like the lower Jungermanniaceæ, it must have been at a very early period, before the sporogonium of the latter had reached its present stage of development.

Leitgeb[1] has already called attention to the connection of *Anthoceros* with the Jungermanniaceæ, and the evolution of the foliose forms of the latter group from the thallose forms is easily demonstrated.

We may then pretty safely assume that the primitive liverworts were thallose forms not unlike such existing forms as *Metzgeria*, or the prothallium of an *Osmunda*, and that from these, three stocks diverged, the Ricciaceæ (including Marchantiaceæ), the Anthoceroteæ, and the foliose Jungermanniaceæ. The first and third of these groups forming the great bulk of the living forms are to be regarded as specialized branches that end blindly; the second, however, is especially important from a morphological standpoint, as it probably represents to a considerable degree, the ancestral form from which both the true mosses and the Pteridophytes have sprung.

The Anthoceroteæ[2] differ remarkably from the other liverworts, especially in the development of the highly specialized sporogonium. This finds its nearest homologue, not among the Hepaticæ, but in the lowest order of the true mosses, viz.:

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[1] Untersuchungen über die Lebermoose, Vol. V, pp. 8–9.

[2] Leitgeb, l. c.

the Sphagnaceæ. The close similarity in the development of the sporogonium in these two groups, can only be explained on the assumption of a common origin, and this is strengthened by the fact that the protonema of *Sphagnum* is a large, flat thallus instead of the filamentous form common to most mosses. In short, *Sphagnum* forms a link between *Anthoceros* and the true mosses.

This is true of the protonema, as well as the sporogonium, for while the younger protonema is at first a simple flat thallus, later there may grow out from its margin filaments which have all the characters of the ordinary protonemal branches of the higher mosses, including their peculiar oblique septa. These filamentous branches, as well as the leafy stem, are secondary, and it is difficult to see how we can assume that the former represents the primitive condition, as Goebel[1] and Bower[2] assert. It seems much more in accordance with the facts to believe that the flat thallus represents the primitive form of all, and that in the mosses, as the leafy branches bearing the sexual organs became more and more prominent, the large prothallium-like protonema gradually became lost, being replaced by the secondary filamentous form found in most mosses.

The foregoing attempt to point out the connection of the different groups of the bryophytes may be illustrated by the diagram on the opposite page.

The probable connection of the Anthoceroteæ with the Filicineæ has been noted by several investigators,[3] but the assumption has been usually made that the relationship must be sought with the Leptosporangiatæ, as these have been regarded as the lowest of the forms. Of the leptosporangiates the Hymenophyllaceæ have usually been regarded as the most primitive, this opinion being based mainly upon the delicate character of the sporophyte. The most recent investigations, however, do not bear this out, and the attempt of Prantl[4] to homologize the sporogonium of *Anthoceros* with the sporophyte of *Hymenophyllum* involves such an amount of pure speculation and so little real morphological correspondence as to be very far from convincing.

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[1] Morphologische u. biologische Studien: Ann. du Jardin botanique de Buitenzorg, Vol. VII, p. 115.

[2] Annals of Botany, Vol. III, No. 11, p. 372.

[3] Leitgeb, l. c., Vol. VI, p. 60.—Prantl, Hymenophyllaceæ, p. 62.

[4] L. c., p. 62.

From a very careful study of the question, the writer[1] was led to a very different view as to the relative position of the different groups of the Filicineæ, and gave what seemed to him strong evidence in favor of considering the eusporangi-

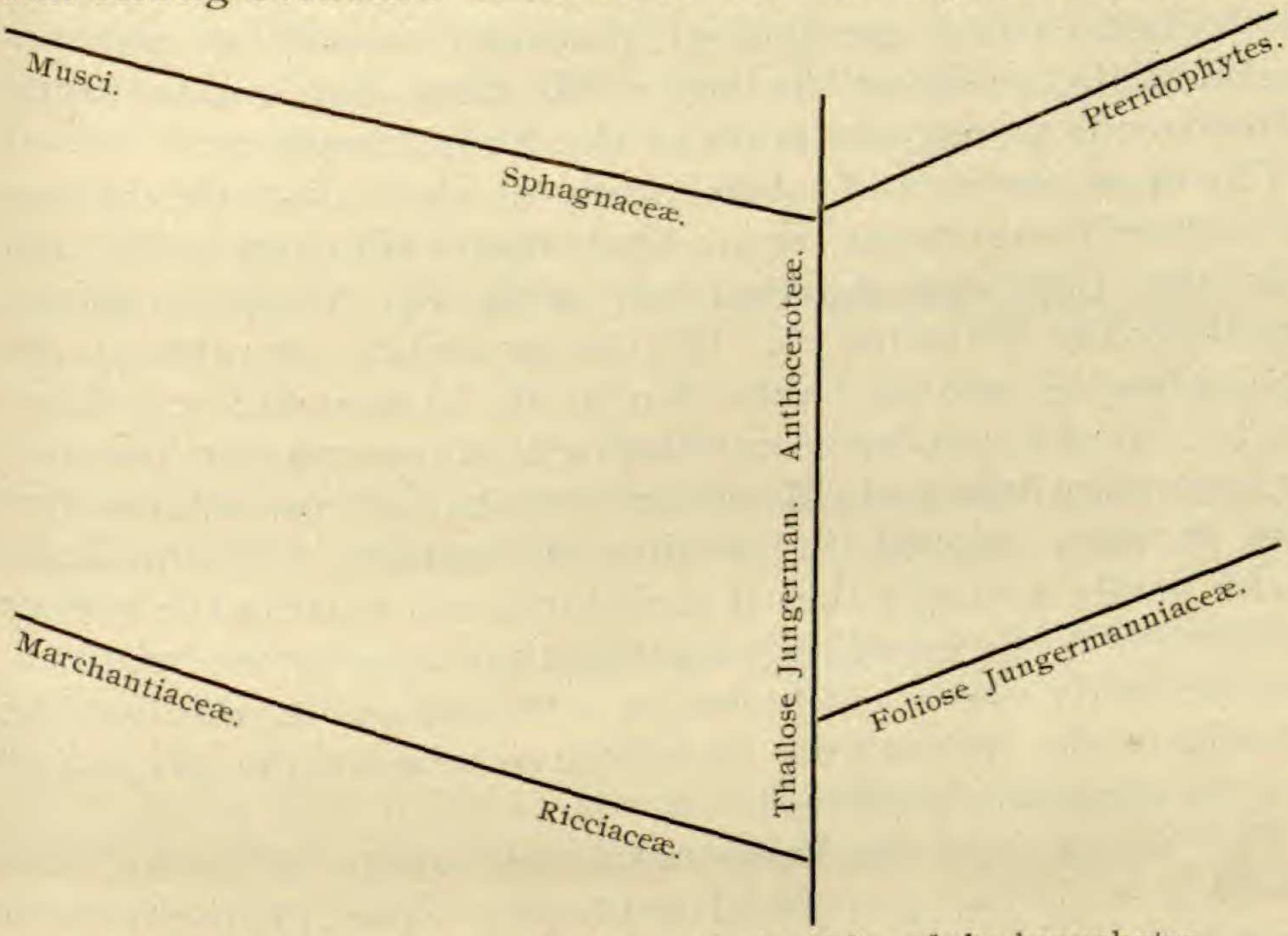

Diagram 1, illustrating the inter-relationships of the bryophytes.

ate forms, which hitherto were regarded as the highest of the ferns, as the primitive forms from which the Leptosporangiatæ have been derived. Ophioglossum was considered to be the nearest of the existing forms to this ancestral form, so far as can be judged from a study of the structure of the sporophyte.

Of the three classes of the pteridophytes, the ferns form a very large majority and constitute the prevailing type of the existing forms. If we compare the number of species in the three classes, we shall find that the Filicineæ comprise at least 90 per cent. of living forms, and that of the 3000 or more species of ferns an overwhelming majority belong to one family—the Polypodiaceæ. This fact, in connection with the highly differentiated sporangium, and other structural peculiarities, led me to express the opinion that the Leptosporangiatæ (of which the Polypodiaceæ are the type), instead of representing the primitive group of ferns, were in fact a com-

[1] Affinities of the Filicineæ, p. 3.

paratively modern, specialized group, comparable to the leafy liverworts or the true mosses. There is no geological evidence to show that the true leptosporangiate ferns were ever much more numerous or better developed than at the present time. On the other hand, the geological record, as well as embryological study, so far as the latter has been applied to them, points to the primitive nature of the Eusporangiatæ.

The most recent and careful study of the carboniferous and pre-carboniferous ferns, show that their affinities were not with the Leptosporangiatæ, but with the Eusporangiatæ, especially the Marattiaceæ. Forms probably referable to the Ophioglosseæ, and probably also to the Osmundaceæ,[1] have also been found, but no unmistakable leptosporangiate remains are known until the early Mesozoic formations, from which time they increase rapidly in number and variety. Solms-Laubach[3] justly remarks that if such forms did exist in the earlier formations, it is exceedingly strange that, among the innumerable perfectly preserved leaves, a structure so durable as the annulus of the sporangium should have failed to be preserved in a recognizable condition.

The ontogeny of the Eusporangiates, so far as known, harmonizes with the geological evidence. The prothallium is more massive, and longer-lived than in the leptosporangiates, in this respect approaching the liverworts, and the sexual organs show points of primitive structure. Unfortunately the embryogeny is scarcely at all known in any of the homosporous forms, which are presumably the most primitive and approach most nearly the ancestral type.

From a series of investigations recently completed by the writer, it appears that the Osmundaceæ are about midway between the true Eusporangiatæ and the Leptosporangiatæ, both in regard to the prothallium and the embryo. The intermediate character of the tissues of the sporophyte has already been repeatedly called attention to by various writers. The prothallium resembles to a remarkable degree that of certain liverworts, notably *Dendroceros*, and the sexual organs approach in certain respects the Marattiaceæ, but also recall *Equisetum* and even certain bryophytes. The embryo is noticeable on account of the large size of the foot and its long depend-

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[1] Solms-Laubach: Palæophytologie, p. 156.
[2] Bower: Annals of Botany, May, 1891.
[3] L. c., p. 156.

ence upon the prothallium, as well as the great development of the calyptra, all of which are evidences of the primitive character of the group, and in all of which, so far as known, it approaches the Eusporangiatæ. An interesting point noted was the fact that the primary root grows from a single tetrahedral apical cell, as in all of the Filicineæ except the Marattiaceæ and *Isoetes*, while the later roots, at least of the two species studied, *O. Claytoniana* and *O. cinnamomea*, possess a four-sided pyramidal apical cell. This seems to indicate that the former is the primitive form which has been retained in all except the Marattiaceæ and the probably allied *Isoetes*. Whether this state of things obtains in the embryo of the former of these is not known, but it is not impossible; in the latter a trace of this is sometimes seen in the very earliest stages of the embryo, but is lost before the root is fully grown.[1]

In the course of these investigations points of resemblance, both in the prothallium and sexual organs were noted, that recalled the corresponding points in *Equisetum*. So numerous were these, that it led to a belief of a nearer relationship between the Equisetineæ and Filicineæ than is usually maintained, and to warrant the possible union of the two classes into a group opposed to the Lycopodineæ. Van Tieghem[2] has called attention to correspondences in the sporophytes of *Equisetum* and *Ophioglossum* which confirm this view. It is even possible that this might be carried so far as to assume a common origin for these two classes, distinct from that of the Lycopodineæ which in some respects recall rather the true mosses than the liverworts. One great difficulty in dealing with the Lycopodineæ, and especially the Equisetineæ, is that they are degenerate forms which have lingered after their larger and better organized kindred have disappeared, and it is difficult to judge which are primitive and which secondary characters. Certain it is, that the investigated species of *Lycopodium*[3] differ more from *Equisetum*, than does the latter from the homosporous Filicineæ. Still we are not yet in a position to speak positively on this point.

Of the true leptosporangiate ferns, the reasons already given

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[1] Campbell: Annals of Botany, Vol. V, No. 19, p. 243.

[2] Unfortunately the paper was not accessible.

[3] Treub: Études sur les Lycopodiacées, Ann. du Jardin botanique de Buitenzorg, Vols. 4, 5, 7.

seem to warrant the assumption that in the Polypodiaceæ we have to do with a group of comparatively modern forms that have arisen from the more ancient Eusporangiatæ through the Osmundaceæ, Gleicheniaceæ and Cyatheaceæ, which families constitute a quite natural series. The two families, Hymenophyllaceæ and Schizæaceæ, while evidently connected with the lower members of this series, seem to form two offshoots from the main line of ascent, and the former is probably a degenerate group whose peculiarities are largely due to the effects of environment. The affinities of the Hymenophyllaceæ seem to be with the Gleicheniaceæ and Osmundaceæ. The form of the sporangium and spores, as well as the prothallium and sexual organs, is of the type found in these groups. The branching filamentous prothallium, upon the importance of which too much stress has been laid, is by no means rare in *Osmunda Claytoniana* under certain circumstances, and the form of the sexual organs is very similar.

As to the sporophyte, the Ophioglosseæ form a natural series with *Ophioglossum* at the bottom, and such species of *Botrychium* as *B. Virginianum* at the top, the latter connecting the group with the Osmundaceæ.

The Marattiaceæ, as might be expected of such ancient forms, show affinities with both the Osmundaceæ and Ophioglosseæ, and may perhaps be regarded as a branch of the original stock that, beginning very far down, reached its maximum development in the Carboniferous era, and then declined. Whether, as suggested by Bower,[1] the spermaphytes have arisen from the same stock, must at present remain conjectural.

The forms hitherto discussed are the so-called isosporous forms. Among the existing pteridophytes, however, are four very distinct groups in which spores of two kinds are found, viz.: Selaginelleæ, Isoeteæ, Marsiliaceæ, and Salviniaceæ. The first of these is evidently enough related to *Lycopodium*, and the third to the Polypodiaceæ; but the affinities of the others are not so clear. The Salviniaceæ, while clearly enough belonging to the Leptosporangiatæ, and related to the lower members of the series, still are so peculiar that it is not easy to decide where they should be placed. Prantl[2] suggests the Hymenophyllaceæ as their nearest allies, and prob-

[1] Annals of Botany, Vol. III, p. 387.
[2] The Schizæaceæ, p. 153.

ably either these or the Schizæaceæ are to be so considered. *Isoetes* is even more difficult to place. It is unquestionably the nearest among living pteridophytes to the spermaphytes, but with what group of homosporous ferns it is most nearly related, is hard to say; for while showing evident relationship to several forms, they are in widely separated groups. On the whole, the evidence is in favor of regarding it as nearest the Marattiaceæ; but this is liable to be changed when the embryogeny of the latter is known, and the life history of the Ophioglosseæ. (See diagram 2.)

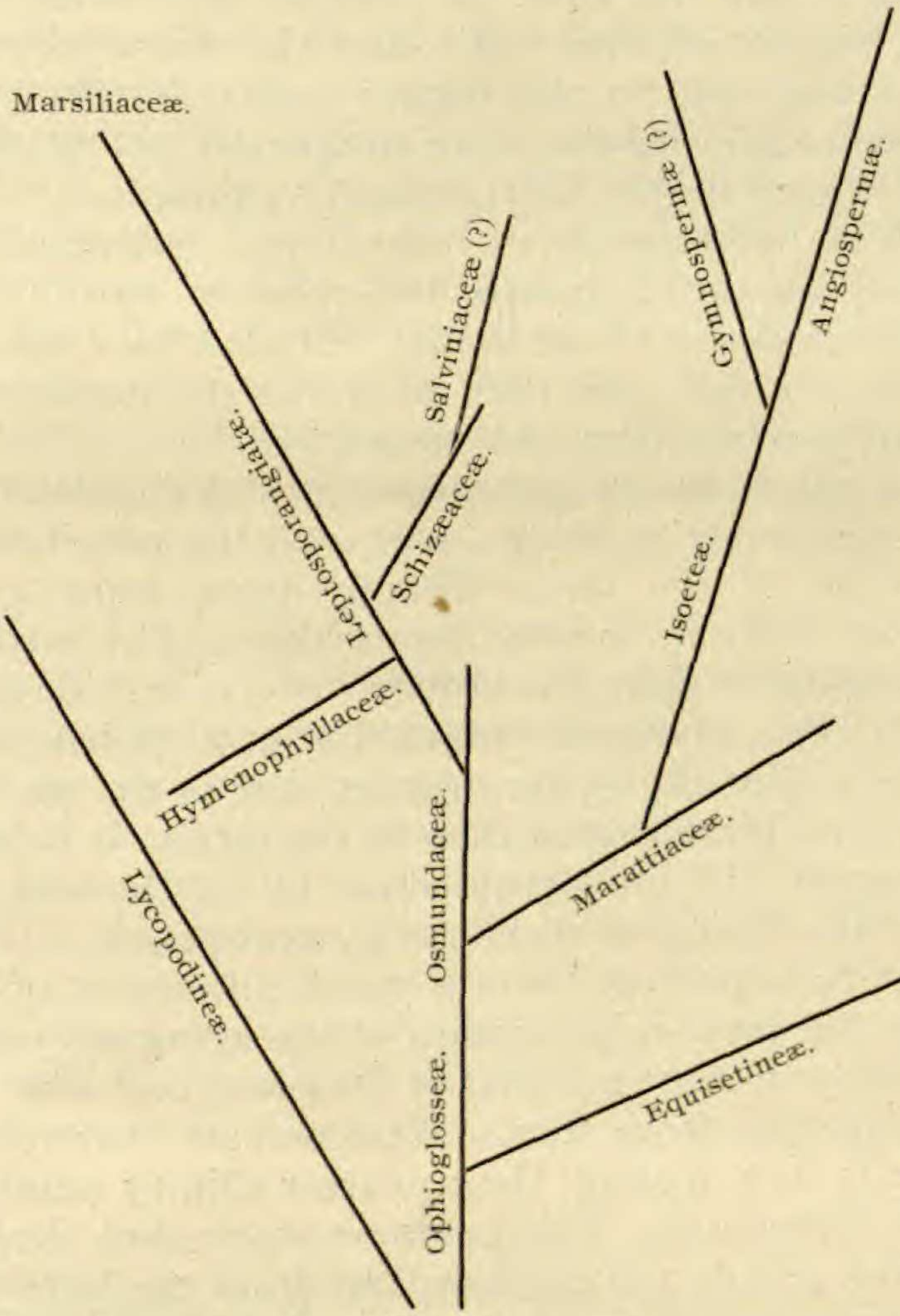

DIAGRAM 2, illustrating the ontogeny of the vascular cryptogams and spermaphytes.

The tendency toward the separation of the sexual organs, occasionally found in nearly all forms examined, occurs regu-

larly in *Equisetum* and many Polypodiaceæ. This tendency has been attended by a greater and greater reduction of the prothallium, which finally, in such forms as *Isoetes*, has lost all power of independent existence, and serves simply to nourish the sporophyte until it can live alone. In these two, the sex of the prothallium is already indicated by the two sorts of spores. This carried a step further resulted in the macrospore being retained permanently within the sporangium which did not separate from the sporophyte until the prothallium was developed.

At first, as is still the case in *Ginkgo*[1] and some cycads, fertilization was not effected until after the sporangium (seed) became detached; but in the higher forms, fertilization and the formation of the embryo were completed before the seed ripened, as is seen in the Abietineæ, for example.

Inasmuch as heterospory was developed independently in several widely separated groups, the question naturally arises whether the formation of seeds may not also have taken place in more than one line, and that all of the spermaphytes have not necessarily arisen from the same stock.

The great gap between gymnosperms and angiosperms it is at present impossible to bridge over, and the possibility of a separate origin of the latter directly from some group of pteridophytes is by no means improbable. The writer's recent investigations upon the embryo of *Isoetes*[2] have shown that it much more nearly resembles that of a typical monocotyledon than it does the gymnosperms, and as the prothallium is hardly more differentiated than in the latter, it is about as easy to imagine the monocotyledons to be derived directly from forms like *Isoetes* as from the gymnosperms.

As might be expected, there is much difference of opinion concerning the inter-relationships of the spermaphytes. The view ordinarily accepted is that of Strasburger,[3] who derived the gymnosperms from forms intermediate between ferns and lycopods, but having their nearest affinity among living forms with *Selaginella*. This common stock then divided into two branches, cycads and conifers, and from the latter through the Gnetaceæ, were derived the dicotyledons, from which as a degenerate group the monocotyledons have descended.

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[1] Goebel: Outlines, p. 338.
[2] The life history of Isoetes echinospora, Ann. of Bot. Vol. V. No. 19.
[3] Coniferen und Guetaceen, p. 258.

Kny[1] claims a distinct origin for the two divisions of the angiosperms. He says, "The two principal divisions of the angiosperms, dicotyledons and monocotyledons, represent two great independent lines of development, whose origin reaches at least as far back as the vascular cryptogams, if not lower." He is inclined with Strasburger to connect conifers and dicotyledons with the Lycopodineæ, and would derive the monocotyledons directly from the ferns.

Prantl's[2] views are much the same as Kny's, except that possibly a part of the dicotyledons have a common origin with the monocotyledons.

From the evidence at present available, both of embryology and palæontology, the assumption of a separate origin for the two groups of the angiosperms is certainly unwarrantable. In all forms yet investigated, the uniformity in the essential structure of the flowers, and especially the development of the embryo-sac, points unmistakably to a common origin. It may be that further investigations upon the lower members of both groups may modify this view, but that such extraordinary correspondence as exists in the formation of the embryo-sac, the structure of the egg apparatus, the fusion of the endosperm nuclei, etc., could have arisen independently in the two groups is inconceivable.

On the other hand, the evidence for a direct connection of gymnosperms and angiosperms, is not entirely convincing, and the possibility of a separate origin for these two groups is by no means unlikely—nay, seems quite probable.

Whether the origin of the angiosperms is to be looked for directly from the Filicineæ, through such forms as *Isoetes*, or from forms higher up like the cycads, can only be satisfactorily answered after many forms have been thoroughly studied. As yet our knowledge of the embryology of the cycads and the simplest angiosperms is too incomplete to make an answer to this question more than a mere conjecture.

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[1] Entwickelung der Parkeriaceen, p. 61.
[2] Hymenophyllaceæ, p. 68.